

## The taxonomic status of the shrew of St. Lawrence Island, Bering Sea (Mammalia: Soricidae)

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*Abstract.*—Shrews of the subgenus *Otisorex* inhabit two islands in the Bering Sea, within the limits of the former Beringian Refugium. Whether those taxa represent independent species, or subspecies of the nearctic *Sorex cinereus* Kerr, has remained uncertain. The karyotype ( $2N = 66$ , FN autosomes = 70) of one of these, described as *Sorex jacksoni* Hall et Gilmore from St. Lawrence Island, has been defined and compared with that of *S. c. cinereus* on the Alaskan mainland, from which it could not be distinguished. No differences could be discerned between the two taxa in structure of the glans penis or in relationships of the medial tines of the incisors. The shrew on St. Lawrence Island is regarded as being a subspecies of *S. cinereus*, for which the designation *S. c. jacksoni* Hall et Gilmore is applicable. A review of published karyograms and other information supports the concept that no species of the subgenus *Otisorex* is holarctic.

*Sorex cinereus* Kerr has the most extensive geographic range of any species of shrew in the Nearctic, occurring in North America from approximately lat. 35°N to the northern shores of Alaska and Canada (Hall 1981, map 14). Records of Rancho-labrean age indicate that its distribution had been more extensive in the southern regions of the continent (Kurtén & Anderson 1980: 105). The fossil record of that species dates from deposits of late Mindel-Kansan time, and possibly earlier.

Diverse interpretations concerning the taxonomy and the geographic ranges of some shrews of the *Sorex cinereus*-group (subgenus *Otisorex*) have been given in the recent literature, especially relating to the northern forms. Hall (1981) distinguished 12 nearctic subspecies of *S. cinereus*, including *S. c. jacksoni* Hall et Gilmore, on St. Lawrence Island (Bering Sea), and *S. c. ugyunak* Anderson et Rand, which inhabits mainly the treeless regions of the continent

from northwestern Alaska eastward to the western shores of Hudson Bay and Foxe-Basin. Another of the group, *S. pribilofensis* Merriam, occurs on St. Paul Island, Pribilof Islands (Bering Sea) (Hoffmann & Peterson 1967). In Eurasia, Stroganov (1956) described *S. c. portenkoi* from the vicinity of Anadyr' (Chukotka) (approx. 64°40'N, 177°20'E), providing the first indication that *S. cinereus* might have an holarctic distribution. Two additional subspecies have been recognized in northeastern Eurasia: *S. c. camtschaticus* Iudin, 1972 (type locality: Kambal' Bay, Ust'-Bol'sheretsk region, Kamchatka) (approx. 52°45'N, 156°30'E), and *S. c. leucogaster* Kuroda, 1933 (syn. *S. beringianus* Iudin, 1967) (type locality: Paramushir Island, Kurile Islands).

On the basis of morphometric analysis, van Zyll de Jong (1982) tentatively considered that *S. cinereus*, *S. jacksoni*, and *S. pribilofensis* are independent species. According to his concept, *S. jacksoni* would be

holarctic in distribution, with *S. j. jacksoni* on St. Lawrence Island, *S. j. ugyunak* in northern North America, and *S. j. portenkoi* and *S. j. leucogaster* in Eurasia. The taxon previously designated *S. c. camtschaticus* was considered also to represent a distinct species. The results of van Zyll de Jong's (1991) further analyses of cranial characters were taken to be compatible with those taxonomic conclusions, except that *leucogaster* also was regarded as being an independent species. Van Zyll de Jong pointed out that his conclusions were tentative, and that study of other taxonomic criteria, particularly cytogenetic and biochemical, was needed. He earlier (1982) noted that "clarification of phallic morphology is needed." Hutterer (1993) acknowledged van Zyll de Jong's concept that *ugyunak* may be specifically distinct from *cinereus*. Junge & Hoffmann (1981) considered *S. jacksoni* and *S. pribilofensis* (designated by them as *S. hydrodromus* Dobson) to be distinct from *S. cinereus*. Okhotina (1984) retained the Eurasian taxa as subspecies of *S. cinereus*. A different concept was presented by Ivanitskaia & Kozlovskii (1985), who proposed on the basis of chromosomal criteria that *S. cinereus* does not occur west of Bering Strait. They regarded *S. c. ugyunak* (without karyological data) as being a distinct species with an holarctic distribution, represented in Eurasia by *S. u. portenkoi*. Zaitsev (1988) pointed out that in such case the trivial name *ugyunak* would have to be replaced by *portenkoi* on grounds of priority. In their review of the systematics of mammals of the USSR, Pavlinov & Rossolimo (1987) concluded that *S. cinereus* does not occur in Eurasia, and that no species of the subgenus *Otisorrex* is holarctic. They distinguished three palaeartic taxa in that subgenus: *S. leucogaster*, *S. ?portenkoi*, and *S. camtschaticus*.

To contribute towards a resolution of some of the taxonomic uncertainties involving shrews of the *cinereus*-group, we describe here the karyotype of *S. c. cinereus* on the basis of shrews collected on the

Alaskan mainland, and compare that of *S. c. jacksoni* (Fig. 1) on St. Lawrence Island. The structure of the glans penis and other taxonomic characters are also compared. Our attempt to collect *ugyunak* in the vicinity of Barrow, Alaska, during August 1994 was unsuccessful, and its karyotype has not been defined. Indications of its intergradation with *S. c. cinereus* along the northern front of the Brooks Range, arctic Alaska, are briefly discussed.

### Material and Methods

For convenience, and with respect to our conclusion concerning the status of one of the taxa studied, we apply the nomenclature of Hall (1981) for subspecies of *Sorex cinereus*. The specimens examined consisted of 239 shrews of the *S. cinereus*-group, collected by us and coworkers in Alaska during the period 1949–1975 and by us during 1980–1994. Specimens of the taxa considered here included *S. c. cinereus*, 90; *S. c. jacksoni*, 77; *S. c. hollisteri* Jackson, 58; and *S. c. ugyunak*, 14, along with measurements of nine additional specimens for which skulls were not retained. Standard data were recorded for all specimens collected, as well as information about reproductive status; skulls or skeletons were routinely prepared. Since many of the shrews were collected primarily for helminthological investigations, skins were prepared only as time permitted; nonetheless, small series were available for all of the taxa considered. For examination of the glandes, entire penes were usually fixed in extended condition in 10% formalin solution. One each from *S. c. cinereus* and *S. c. jacksoni* was stained in acetic carmine, dehydrated in ethanol, and cleared in terpineol for examination. Two additional male specimens of *S. c. jacksoni* (August 1957 and May 1993) were used only for the study of the genital organs. Measurements of larger cranial dimensions were made by means of a dial-caliper, graduated in tenths of millimeters and provided with a fine adjustment.





Fig. 1. *Sorex cinereus jacksoni*. Photographed on 15 June 1992, approximately 1 km west of Savoonga, St. Lawrence Island.

In measuring tooth-rows and other features of small size, a stereoscopic microscope with a calibrated scale, graduated in tenths of millimeters, was used. Degrees of latitude and longitude given below are approximate.

Chromosomes were examined from 7 specimens of *S. c. cinereus* collected in Alaska as follows: 1 female (August 1972), Chena Hot Springs Road (64°53'N, 147°W); 1 female (August 1993), 6 km NE of Palmer (61°39'N, 149°13'W); 1 female, 1 male (August 1991), 16 km N of Gakona Junction Village (62°24'N, 145°22'W); 1 male (August 1993), 35 km S of Paxson (62°52'N, 145°29'W); 2 females (August 1993), 17 km S of Copper Center (61°51'N, 145°15'W). From *S. c. jacksoni*, preparations were made from 5 adults and 2 embryos collected near Savoonga, St. Lawrence Island (63°42'N, 170°29'W): 3 males (June 1980, June 1984, June 1987); 1 female (June 1987), and 1 female (June 1988), with one female and one male embryo.

Cells from marrow and lymphatic tissue

were treated with colchicine and hypotonic solution, centrifuged, fixed, and placed on slides in the field, where also testicular tubules were fixed and stained in acetic orcein, employing standard karyological procedures. Most preparations were stained in the laboratory at the University of Washington; in some cases, only orcein-staining was feasible. Banding of chromosomes was produced by application, for G-banding, of the method of Seabright (1972), and for C-bands, that of Sumner (1972). Chromosomes were counted and evaluated in intact cells in metaphase; at least 10 cells were photographed from each animal, from which, in non-banded complements (standard Giemsa stain), measurements were made as recommended by Levan et al. (1964). In karyograms constructed for comparisons, arm-ratios and size were the bases for assembling pairs of non-banded chromosomes. Those with G-bands were distinguished according to banding pattern and size; C-banded chromosomes were identified by size and by location of centromeric heterochromatin. The fundamental number

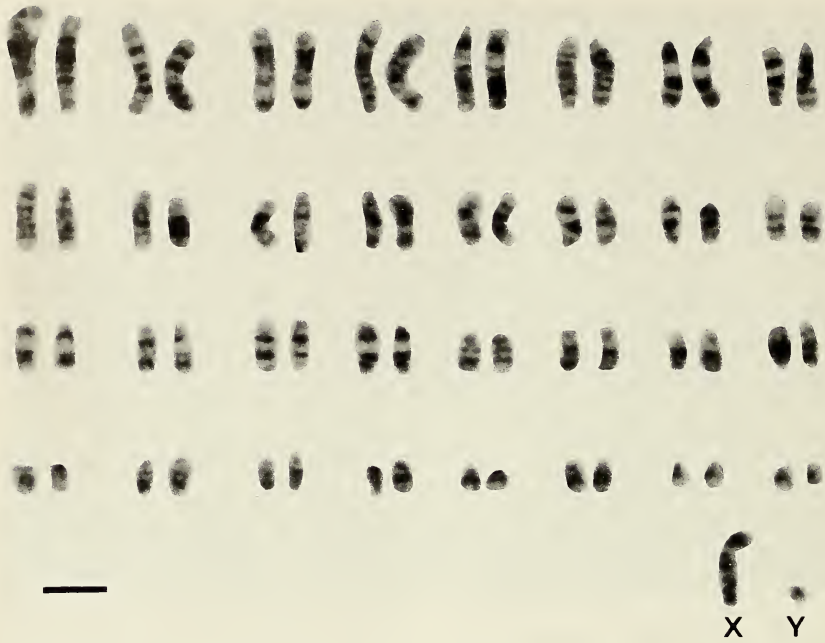


Fig. 2. Karyogram of *Sorex c. cinereus*, male. Giemsa-banding. Scale-bar represents 5 micrometers.

(FN) of major chromosomal arms was determined according to the method of Matthey (1945).

Voucher-specimens of the two subspecies of *Sorex cinereus* have been deposited as follows: Burke Memorial Washington State Museum, University of Washington, Seattle, No. 39403 (*Sorex cinereus jacksoni*); and Museum of Southwestern Biology, University of New Mexico, Albuquerque, Nos. 69701, 69702, 69703 (*Sorex cinereus jacksoni*), and Nos. 69704 and 69705 (*Sorex cinereus cinereus*).

### Results

**Karyograms.**—*Sorex cinereus cinereus*: The diploid complement (66) consisted of the following: autosomes—centromere in subterminal to near-terminal region (pairs 1–31) (range of arm-ratio 3.8 to 12.0); centromere in median region (pair 32) (arm-ratio 1.2 to 1.4); sex chromosomes—X-chromosome with centromere in submedian region (range of arm-ratio 2.0 to 2.7), in metaphase usually approximately equal in

total length to that of largest autosomes; Y-chromosome with centromere in subterminal region (arm-ratio not determined). The Y-chromosome (in metaphase) was the smallest of the complement (Fig. 2). The FN was calculated to be 70. The distribution of constitutive heterochromatin in the diploid complement (C-banded) is shown in Fig. 3.

Meylan (1968) preliminarily reported a diploid number of 66 and FN of 70 for two female specimens of *S. c. cinereus* collected in the Province of Ontario, Canada; that publication appeared later than his description and illustration of the chromosomal complement (Meylan 1967). Recently, Volobouev & van Zyll de Jong (1994) provided karyograms of a male shrew of that species from Pennsylvania. We conclude that the aforementioned specimens, all collected near the eastern limits of the range of *S. c. cinereus*, were karyotypically identical with those obtained in Alaska. The karyotype of *S. c. cinereus* is probably uniform throughout its geographic range.

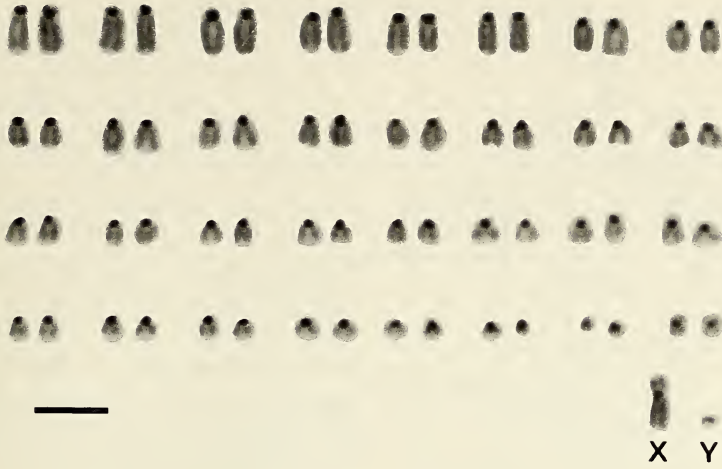


Fig. 3. Karyogram of *S. c. cinereus*, male. C-banding. Scale-bar represents 5 micrometers.

*Sorex cinereus jacksoni*: The diploid complement (66) consisted of the following: autosomes—centromere in subterminal to near-terminal region in 31 pairs (1–31) (range of arm-ratio 3.6 to 13.6); centromere in median region (pair 32) (arm-ratio of 1.1 to 1.6); sex chromosomes—X-chromosome with centromere in submedian region (range of arm-ratio 1.7 to 2.6); Y-chromosome (metaphase) was the smallest in the complement (Fig. 4). As in *S. c. cinereus*, the FN of *S. c. jacksoni* was 70. The preparations from all but two were processed

with acetic orcein; G-banded chromosomes were not of uniform quality, but homologues could be identified and compared by selecting the best individuals from each preparation. We were unable to discern karyological differences between *S. c. cinereus* and *S. c. jacksoni*.

*The glans penis*.—The glans penis of *S. c. cinereus*, first illustrated by Iudin (1969), differs in form from that of any other species of *Sorex* for which information is available. We compared the glandes of six specimens of *S. c. jacksoni* with four from *S. c.*

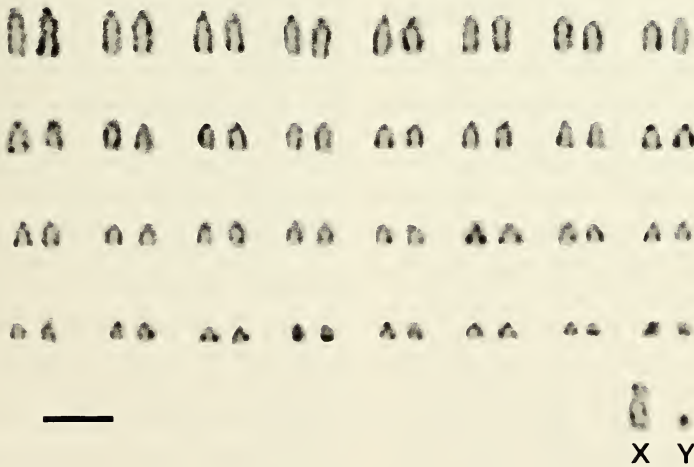


Fig. 4. Karyogram of *S. c. jacksoni*, male. Orcein. Scale-bar represents 5 micrometers.



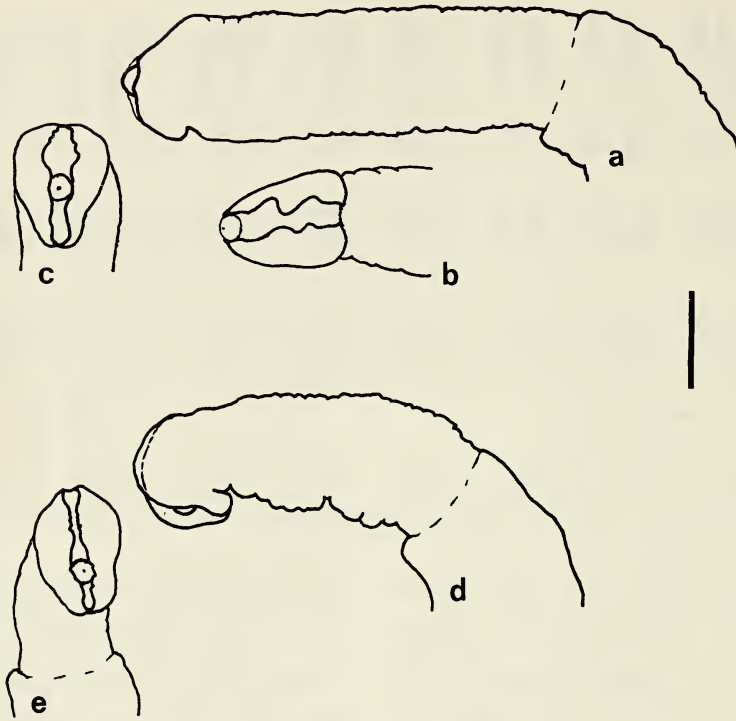


Fig. 5. Glans penis of *S. c. cinereus* (a–c) and *S. c. jacksoni* (d–e). a, lateral view of penis; b, dorsal view of glans; c, en face view of glans; d, semi-lateral view of penis; e, en face view of glans. Scale-bar represents 1 millimeter.

*cinereus*. The penes of both were of approximately uniform diameter distally, and were about 1 to 1.5 mm in diameter just posterior to the glans. When not fully extended, the surface of the penis immediately posterior to the glans exhibited folds, some of which extended around the entire circumference of the organ. In our specimens, such folding of the superficial tissue was not so strongly defined as was portrayed by Iudin (1969). In lateral view, the anterior surface of the glans appeared truncate to curved, with its distal portion projecting ventrad or ventroposteriad, depending on degree of contraction (Fig. 5a). In en face view, the glans was more or less cordate in shape, and was bisected by a medial groove extending anteriad and ventrad from the dorsal surface to the end of the ventral protrusion (Fig. 5c). The orifice of the urethra was situated in that groove near the middle

of the anterior surface of the glans, opening at the apex of a small papilla, which in some cases protruded slightly above the surrounding surface of the glans (Fig. 5a, b). In one specimen, the end of the urethra protruded from the papilla, appearing as a processus urethrae; probably, however, it was a structural artifact, produced in the process of removing the organ for fixation. It was evident that the glans is subject to muscular control, which may cause slight modification in its shape. The glandes of *S. c. jacksoni* (Fig. 5d, e) were indistinguishable from those of *S. c. cinereus*. A fully relaxed penis of *S. c. jacksoni* was 19 mm long from its point of attachment to its distal end. The animal (TL 91 mm) was in breeding condition, with testes measuring  $5 \times 3.5$  mm. Also compared was the glans penis of one specimen of *S. c. hollisteri* collected at Hooper Bay (Kuskokwim-Yukon

delta) (61°27'N, 166°W) in May 1966 and preserved intact in formalin solution. The glans was indistinguishable from that of *S. c. cinereus* and *S. c. jacksoni*.

*Other morphological characters.*—Cranial characters of shrews of the *cinereus*-group have been compared by van Zyll de Jong (1976, 1982, 1991). We found in *S. c. jacksoni* that the accessory medial tines of the incisors, also important taxonomically (Junge & Hoffmann 1981; Dannelid 1989, 1994) did not differ in position from those of *S. c. cinereus*, *S. c. hollisteri*, and *S. c. streator*, from the Alaskan mainland, but were perhaps slightly greater in length. Like some other small mammals inhabiting islands in the Bering Sea, *S. c. jacksoni* is somewhat larger than shrews representing the various subspecies of *S. cinereus* on the Alaskan mainland. External measurements (Table 1) were based on a series of 38 males and 23 females, judged to be adults on the basis of the reproductive status of those collected during July and August, and on the large size of those obtained during September through November. Another series of 23 specimens collected in June, considered to be over-wintered adults, averaged somewhat smaller (Table 1). Compared with specimens of *S. c. cinereus* collected in east-central Alaska during August, mean total lengths of *S. c. jacksoni* were greater and tail-length was less. Weights were not obtained for the series of *S. c. cinereus*. Youngman (1975) found weights of nine specimens from the southern Yukon Territory to range from 3.1 to 5.1 g ( $\bar{X}$  = 4.3 g). Mean total length for a series of 18 specimens of *S. c. hollisteri* (one collected in June, the remainder in August) from Napaskiak (62°41'N, 161°54'W) on the lower Kuskokwim River was similar to that of males of *S. c. jacksoni*; *S. c. jacksoni* had a shorter tail, and the mean body-weight was greater (Table 1). For the series of *S. c. jacksoni* collected in summer, weights of 13 non-pregnant females ranged from 4.8 to 7.3 g ( $\bar{X}$  = 5.0 g). In 11 pregnant animals,

Table 1.—Body measurements (mm) and weights (g) of some subspecies of *Sorex cinereus*.

Subspecies	Total length			Length tail			Hind foot			Weight		
	n	Range	$\bar{X}$ SD	n	Range	$\bar{X}$ SD	n	Range	$\bar{X}$ SD	n	Range	$\bar{X}$ SD
<i>jacksoni</i> (July–Nov)	31 ♂♂	92–103	97.8 (2.67)	38 ♂♂	32–38	35.2 (1.39)	38 ♂♂	12–13	12.4 (0.44)	35 ♂♂	4.1–7.0	5.5 (0.81)
	17 ♀♀	89–105	99.4 (4.10)	23 ♀♀	32–37	34.5 (1.61)	23 ♀♀	11.5–13	12.3 (0.43)	19 ♀♀	4.3–8.8	6.3 (1.20)
<i>jacksoni</i> (June)	13 ♂♂	91–100	94.9 (3.47)	13 ♂♂	30–38	34.8 (2.34)	13 ♂♂	12–13	12.5 (0.48)	—	—	—
	11 ♀♀	91–104	95.7 (5.60)	11 ♀♀	31–36	34.3 (2.09)	11 ♀♀	12–13.5	12.5 (0.52)	—	—	—
<i>cinereus</i> (10 ♀♀ 2 ♂♂)	12	89–101	93.2 (3.78)	12	36–43	38.5 (2.21)	12	10–13	12.2 (1.06)	—	—	—
<i>hollisteri</i> (8 ♀♀ 7 ♂♂ 3?)	18	91–101	97.7 (2.72)	18	32–41	37.2 (2.19)	18	11–13	11.7 (0.55)	14	3.8–6.5	4.5 (0.75)

the numbers of embryos ranged from 5 to 14, with a mean of about 10 (9.7).

### Discussion

With respect to the relationships and distributional status of shrews of the subgenus *Otisorrex*, two differing hypotheses have been proposed: *Sorex jacksoni* may be an independent species, with three subspecies, *S. j. jacksoni* (St. Lawrence Island), *S. j. portenkoi* (NE Siberia), and *S. j. ugyunak* (tundra of NW North America); *S. pribilofensis* (St. Paul Island), *S. leucogaster* (Paramushir Island), and *S. camtschaticus* (NE Siberia) would each be specifically distinct; or *jacksoni* and *leucogaster* may be closely related if not conspecific, and *ugyunak* would be an independent species, represented in North America by *S. u. ugyunak* and in Eurasia by *S. u. portenkoi*. Since *portenkoi* (a prior name, see introductory remarks) would then replace *ugyunak*, the subgenus *Otisorrex* would be represented in Eurasia by the species *leucogaster*, *camtschaticus*, and *portenkoi*, of which the last would be holarctic. Karyological investigations, although incomplete, have been helpful in resolving some of the questions about conspecificities.

As described and illustrated by Ivanitskaia & Kozlovskii (1985), the karyotype of *portenkoi* ( $2N = 60$ ,  $FN = 60$ ) distinguishes that taxon from *S. c. cinereus* and *S. c. jacksoni* ( $2N = 66$ ,  $FN = 70$ ). The karyogram of *leucogaster*, however, is like that of the latter two taxa with respect to diploid number,  $FN$ , and perhaps morphological characteristics of the chromosomes. Nonetheless, *leucogaster* is considered to be specifically distinct from *S. cinereus* (Ivanitskaia & Kozlovskii 1985, Pavlinov & Rossolimo 1987, van Zyll de Jong 1991). A significant distinguishing character, as shown by Iudin (1969, 1971), is the glans penis of *S. beringianus* Iudin (= *S. leucogaster*), which differs from that of *S. cinereus* in being rounded and smooth, described by Iudin (1969:29) as having "... a mas-

sive, globular, rounded crown," with an apparent corona, and lacking the ventral extension typical of the glans of *S. cinereus*.

Definition of karyotypes can be expected to clarify the affinities of *pribilofensis* and *ugyunak*. We examined the glans penis of only one specimen of *S. pribilofensis*, dissected from an animal preserved in formalin, and it was not suitable for detailed comparison. Some indications exist that *ugyunak* will be found to represent a subspecies of *cinereus*. A converse possibility was indicated in the vicinity of the Mackenzie Delta, Northwest Territories (Canada), where *cinereus* and *ugyunak* appeared to be associated with taiga and tundra, respectively, with no reported evidence of intergradation (Martell & Pearson 1978). With reference to *S. c. cinereus*, Youngman (1975:41) remarked that "Shrews of this subspecies become smaller in a cline from the central Yukon to the northern part of the Territory, where they intergrade with the smaller *S. c. ugyunak*," and evidence for intergradation of *ugyunak* with *cinereus* and possibly with *hollisteri* was reported by Bee & Hall (1956) in northern Alaska. Twenty-three specimens collected by us along the northern margin of the Brooks Range, between about lat.  $67^{\circ}57'N$  and  $68^{\circ}20'N$  (encompassing taiga as well as tundra) were designated *S. c. ugyunak*; body-measurements and cranial dimensions of them were interpreted as indicating intergradation with *S. c. cinereus*. The medial tines of the incisors of those specimens were like those of the latter taxon. (The data concerning *ugyunak* will be reported elsewhere.)

Analysis of morphometric data may define precisely the degree of difference existing among taxa, but does not necessarily provide a basis for establishing taxonomic rank. As well, insular species may present unusual difficulties if conclusions are derived solely from macromorphological data, without consideration of potentiality for genetic drift and of the rate at which morphological divergence may have taken place. The small mammals on St. Lawrence Is-



land, with the possible exception of the varying lemming there, *Dicrostonyx exsul* Allen, have been isolated for only about 10,000 years or less; that island was the last of the Beringian highlands to become separated from the continents by rising sea level at the end of the Pleistocene period (Hopkins 1959, 1976). In addition to the shrew and the varying lemming, the indigenous terrestrial mammals of the island (excluding the arctic fox, *Alopex lagopus* (L.), which immigrates and emigrates freely on the sea-ice) consist of the northern red-backed vole, *Clethrionomys rutilus* (Pallas); the northern vole, *Microtus oeconomus* (Pallas); and the arctic ground squirrel, *Citellus parryi* (Richardson). The mammalian faunas of the other Beringian islands (not including the upper Aleutian Islands) are more depauperate: a single species, *Microtus abbreviatus* Miller, on the St. Matthew Islands; the brown lemming, *Lemmus sibiricus* (Kerr), on St. George Island and *Sorex pribilofensis* on St. Paul Island (Pribilof Islands), and *L. sibiricus* and *Dicrostonyx vinogradovi* Ognev, on Vrangell Island. With the exception of the varying lemmings, *S. pribilofensis*, and *S. jacksoni* (about which questions have remained) all of the small mammals on the Beringian Islands are recognized as being only subspecifically distinct from their precursors on the continents. All but the brown lemmings are characterized in part by larger size, most strongly defined in the voles. *Microtus abbreviatus* on the St. Matthew Islands is not only much larger than any of the continental subspecies (Alaska and NW Canada), but it exhibits the greatest degree of phenotypic divergence among the insular taxa mentioned (Rausch & Rausch 1968). *Microtus oeconomus* on St. Lawrence Island also is very large (TL up to at least 210 mm); only *M. o. koreni* Allen, inhabiting the valleys of the Kolyma and Indigirka Rivers, in Chukotka, approaches it in size. The red-backed vole on St. Lawrence Island (TL up to at least 155 mm) is larger than subspecies of *Clethrionomys rutilus* in either Chukotka or Alaska, approaching the

northeastern Siberian red-grey vole, *C. rufocanus* (Sundevall) in size. Comparisons have shown that the karyotypes of *S. cinereus*, *L. sibiricus*, *M. abbreviatus*, and *M. oeconomus* are indistinguishable from those of conspecifics on the continents (*L. sibiricus* and *M. oeconomus* are holarctic). *Clethrionomys rutilus* is also indistinguishable karyotypically, except that chromosomal polymorphism, involving a Robertsonian rearrangement, was observed among animals collected at one locality (Sevuokuk Mountain) on St. Lawrence Island, possibly indicating that chromosomal evolution is taking place (Rausch & Rausch 1975b). Like *C. rutilus* in Alaska and Chukotka, *C. rutilus* on St. Lawrence Island has a metacentric Y-chromosome (Vorontsov et al. 1978). When the arvicolids were crossed with respective conspecifics from the Alaskan mainland, the offspring were found to be interfertile for numerous generations (Rausch & Rausch 1968, 1975a, 1975b, and unpubl.). Intergrades were bred within each successive generation. Such breeding was carried to about the 30th generation in the case of *C. rutilus albiventer* × *C. r. dawsoni*, and to at least several generations with the other species. With successive generations, the offspring of *M. abbreviatus fisheri* Merriam × *M. a. muriei* Nelson, from the Alaskan mainland, increasingly resembled the latter in size and cranial characteristics (R. L. Rausch, unpubl.). Such investigations involving *S. c. jacksoni* have not been attempted, since shrews are comparatively difficult to breed in captivity. Relative to the biological species-concept, we conclude that none of the aforementioned species, with exceptions as noted, is reproductively isolated.

The varying lemmings on the Beringian Islands, *D. exsul* on St. Lawrence Island, and *D. vinogradovi* on Vrangell Island, are karyotypically distinct (Rausch 1977, Kozlovskii & Khvorostianskaia 1978). Both are restricted to habitat at higher elevations. On St. Lawrence Island, the wet tundra that covers 60% of the surface-area is occupied

by the northern vole and the shrew, and the lowlands of Vrangels' Island are inhabited by brown lemmings. The limitation of varying lemmings to areas of higher elevation on the two islands may be attributable to the competitive superiority of the northern vole and the brown lemming, respectively (Rausch & Rausch 1975a). Among the species on the Beringian islands, *Dicrostonyx* spp. may have been the most ancient colonizers of the highlands that are now islands. Lemmings of the genus *Praedicrostonyx* evidently spread into eastern Beringia more than a million years ago, where they were replaced by *Dicrostonyx* (subgenus *Misothermus*) in pre-Mindel time (Zazhigin 1976). *Dicrostonyx* (subgenus *Dicrostonyx*) first appeared in deposits of Riss age. The degree of karyotypic diversity among Recent varying lemmings and the vast extent of their geographic distribution in the Nearctic (including apparently all of the islands of the Canadian Arctic Archipelago as well as Greenland) are indicative of long isolation of the respective populations. Of the small mammals on the Beringian islands, probably only the varying lemmings had been long established in restricted habitat by the time the mammals of the other species were separated from continental populations at the end of the last glacial period.

In insular populations, phenotypic changes sufficient to permit characterization of subspecies may take place comparatively rapidly [cf. Degerbøl (1939) for *Apodemus sylvaticus islandicus* Thienemann; Huxley (1943) for *Mus musculus* L.; and Cameron (1958) for mammals on Newfoundland]. All of the small mammals on islands within the area of Beringia were described originally as independent species. The period of time elapsing since their separation has been sufficient to mark most of those taxa as different, but only infraspecifically so, from mainland populations. With the exception of the varying lemmings, and possibly *Sorex pribilofensis*, none is known to have become reproduc-

tively isolated during the relatively brief interval since the end of the Pleistocene epoch.

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